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July 1986

TR EL-82-4

Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

AMERICAN OYSTER

Fish and Wildlife Service
U.S. Department of the Interior

Coastal Ecology Group
Waterways Experiment Station
U.S. Army Corps of Engineers

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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Mid-Atlantic)

AMERICAN OYSTER

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

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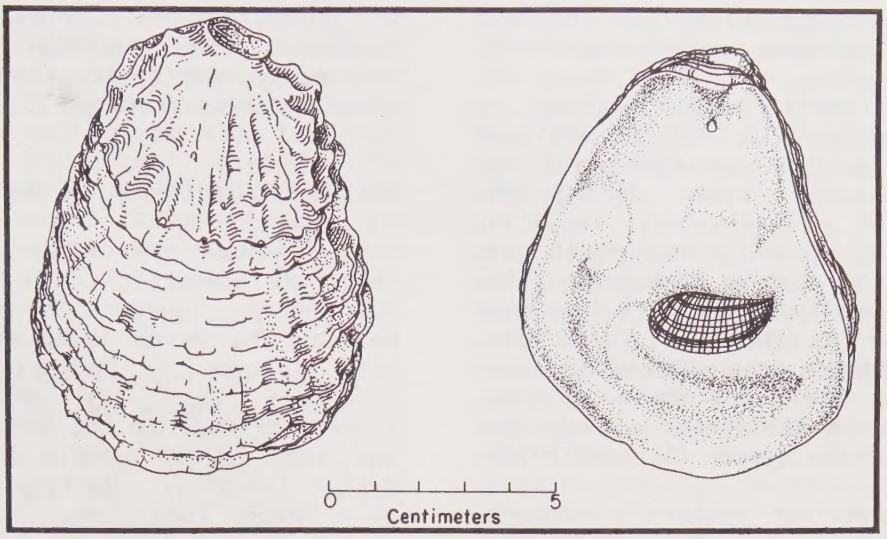

Figure 1. American oyster (Galtsoff 1964).

AMERICAN OYSTER

NOMENCLATURE/TAXONOMY/RANGE

Scientific name . . . . . Crassostrea virginica (Gmelin)
Preferred common name . . . American oyster (Figure 1)
Other common name . . . Eastern oyster
Class . . . . . Bivalvia (Pelecypoda)
Order . . . . . .Mytiloida (Pteroidea)
Family. . . . . Ostreidae

Geographic range: The American oyster lives in estuaries and behind barrier islands along the east coast of North America, from the Gulf of St. Lawrence, Canada, to Key Biscayne, Florida. Its range extends to the Yucatan Peninsula of Mexico and the West Indies to Venezuela. This species was successfully introduced in Japan, Australia, Great Britain, Hawaii, and the west coast of North America (Ahmed 1975). In the mid-Atlantic region, the American oyster is most abundant in Long Island Sound, Delaware Bay, and Chesapeake Bay.

MORPHOLOGY/IDENTIFICATION AIDS

The left valve is almost always thicker and heavier than the right, and more deeply cupped (Yonge 1960; Galtsoff 1964). The oyster is cemented to the substrate on its left valve. Hinge teeth are absent, but a buttress on the right valve fits into a depression on the left. There is no gap between the valves when fully closed.

Shell shape is variable. On hard bottoms, beaks (umbones) usually are curved and point toward the posterior, whereas in silty environments or on reefs, umbones are usually straight. Single oysters from hard substrates are rounded and ornamented with radial ridges and foliated processes (Figure 1), whereas those from soft substrates or reefs are more slender and are sparsely ornamented. Shell thickness also depends on environment. Oysters on hard substrates have thicker and less fragile shells than those on soft substrate. The index of shape (height + width/length) varies from 0.5 to 1.3

in southern populations and from 0.6 to 1.2 in northern populations.

The shell grows along a dorsal-ventral axis, but the angle of the axis is not permanent and may change several times during the lifespan of an individual, resulting in a zigzag pattern. The growth axis may change as much as 90 degrees. The shell is usually 10 to 15 cm long when the oyster is 3 to 5 years old. Although tissue mass reaches an upper limit, the shell continues to grow, primarily in thickness, over the lifespan of the oyster (Stenzel 1971).

The American oyster is monomyarian (anterior adductor muscle has been lost). The interior of the shell has a purple-pigmented adductor muscle scar situated slightly posterior and ventral. A second muscle scar, of the Quenstedt's muscle, is situated ventral to and a short distance from the hinge. The purple pigmentation on the adductor muscle scar distinguishes the American oyster from similar species. In the mangrove oyster (C. rhizophorae) and Pacific oyster (C. gigas), the muscle scar is lightly pigmented and in C. rivularis it is unpigmented. The shell of the mangrove oyster is less plicated than that of the American oyster. There are no other species of Crassostrea sympatric with the American oyster in the Mid-Atlantic region. Species of Crassostrea are distinguishable from species of Ostrea species by the promyal chamber, which is well developed in Crassostrea species, but not in Ostrea. By trapping salt water, this chamber may allow the American oyster to tolerate wider fluctuations in salinity in estuaries.

Crassostrea species are oviparous (gametes are released into the water), whereas Ostrea species incubate fertilized eggs in the mantle cavity. Advanced larvae of American oysters are distinguished from the larvae of other bivalves by length-width measurements and an asymmetric umbo. The dentition on the hinge of the larvae of the American oyster is distinctly different from that in other bivalves (Lutz et al. 1982).

REASON FOR INCLUSION IN SERIES

The American oyster supports an important commercial fishery from the Gulf of St. Lawrence to the Gulf of Mexico, and is an important mariculture species. More oysters are processed than any other single fishery product in the United States, and over 10,000 people work in the oyster industry. Oysters are valued as a luxury food item. The American oyster is the keystone species of a reef biocoenosis that includes several hundred species (Wells 1961). Because the oyster inhabits estuaries, it is particularly vulnerable to urban and industrial disturbances.

LIFE HISTORY

Gametogenesis and spawning are stimulated by changes in water temperature (Kaufman 1978; Andrews 1979a, 1979b; Kennedy and Krantz 1982b). Spawning temperatures differ among populations. Based on spawning temperature, Stauber (1950) recognized three physiological races, one from the Gulf of Mexico that spawns when water temperatures are near 25 °C, and two from the east coast that spawn at 16 °C and 20 °C. Evidence for physiological races also was reported by Loosanoff (1969), who found that gametes of 60% of the oysters from Long Island Sound populations ripened at a water temperature of 15 °C after 45 days, whereas only 20% of the oysters from a New Jersey population had ripe gametes after 72 days at the same temperature. At 18 °C none of the oysters south of New Jersey matured in a holding pond in Connecticut, even after 3 years. In Barnegat Bay, New Jersey, oysters first spawn when water temperature reaches 20 °C, but subsequent spawning

requires water temperatures of at least 22 °C (Nelson 1928). In Delaware, native oysters matured in 150 days at 15 °C (Price and Maurer 1971), which is a much longer time than that reported by Loosanoff (1969). The days required for gonad maturation (D) in Long Island Sound oysters are inversely proportional to temperature (T in °C):

$$D = 4.8 + 4205\ e^{-0.355T}$$

Delaware oysters require six times as long to ripen at water temperatures from 12 to 20 °C as do Long Island Sound oysters (Price and Maurer 1971). In Chesapeake Bay, spawning occurs when water temperatures are 21 to 24 °C, with limited spawning at 15 to 20 °C (Kennedy and Krantz 1982).

The variation in spawning temperature may be caused by other factors. Kennedy and Krantz (1982) postulated that phytoplankton blooms and nutrition may be responsible for stimulating spawning in Chesapeake Bay oysters.

The time and intensity of spawning do not depend directly on tidal cycles (Loosanoff and Nomejko 1951). During low tide, however, the sunlight may warm the water and stimulate spawning (Drinnan and Stallworthy 1979).

Spawning is initiated by one or more males that release their sperm and a pheromone into the water. The females spawn when sperm enter the water transport system (Andrews 1979a), or when pheromone stimulates females to release their eggs in a mass spawning (Bahr and Lanier 1981). Each female produces 23 million to 86 million eggs per spawning; the number is proportional to the size of the individual (Davis and Chanley 1955). Individual fecundities of 15 million to 115 million were cited by Yonge (1960). Females may spawn several times in one season; as the interval between spawnings increases, the number of eggs produced per season decreases (Davis and Chanley 1955). The quantity of sperm produced depends on the quantity of stored glycogen of the male oyster at the beginning of the spawning season (Loosanoff and Davis 1952).

The spawning season is longer in warmer climates: from April to October in the Gulf of Mexico (Hayes and Menzel 1981); but only in July near Prince Edward Island, Canada (Drinnan and Stallworthy 1979). In Long Island Sound, spawning begins around July 1 and lasts into August (Loosanoff and Nomejko 1951). In Chesapeake Bay, Maryland, spawning is from May to September; oysters in shallower water spawn first (Beaven 1955). Oysters at an unusual depth of 40 m in cooler waters of Patuxent River estuary do not release all their gametes during the spawning season (Merrill and Boss 1966). Kennedy and Krantz (1982) documented the spawning season for 18 beds in Chesapeake Bay. Spawning begins in May in some beds, and June in others. Spawning continues into August in most beds and into September in a few (to December in one bed). The spawning season in eastern shore bars extended over a longer period during the early 1960s than in 1977 to 1978. In the James River estuary, Virginia, spawning commences in late May and continues until October (Loosanoff 1932). The eggs hatch about 6 hours after fertilization at water temperatures near 24 °C (Loosanoff 1965a).

Larvae

Oyster larvae are meroplanktonic and remain in the water column for 2 to 3 weeks after hatching (Bahr and Lanier 1981). In Milford Harbor, Connecticut, the larval period is 13 to 16 days at 22 °C (Prytherch 1929). During the planktonic phase, the larvae pass through several stages of development (Carriker and Palmer 1979). After the blastula (3.2 hr),

gastrula (4.5 hr), and trochophore (10 hr) stages (Parrish 1969), the larva secretes a straight-hinge shell and develops a ring of locomotory cilia called the velum. This prodissoconch I larva (also termed straight-hinge larva or veliger) is about 75 µm in diameter. It develops into the prodissoconch II larva (also termed eyed larva or pediveliger), which is characterized by pronounced umbones. This larva is a vigorous swimmer, and has a pair of pigmented eyes and an elongated foot with a large byssal gland (Andrews 1979a). The prodissoconch larva is about 0.3 mm in diameter (Galtsoff 1964).

Young larvae (prodissoconch I) in Little Egg Harbor, New Jersey, stay in the water column about 1.0 m below the surface (Carriker 1951). Older larvae (prodissoconch II) are near the bottom in the halocline of estuaries during flood tide and rise nearer the surface during the ebb tide. The late stage larvae congregate near the bottom of Delaware Bay during slack tide and are distributed throughout the water column during flood tide (Kunkle 1957). Andrews (1979a) doubted the validity of these findings. In the laboratory, older larvae are stimulated to swim by increased salinities and inhibited by decreased salinities (Haskin 1964). Larvae are on the bottom of Milford Harbor, Connecticut, when the current is greater than 0.6 m/sec and drop to the bottom in holding tanks at velocities of 0.3 to 0.5 m/sec (Prytherch 1929). Swimming velocity increases by threefold at a salinity near 100% seawater (Hidu and Haskin 1978). Upward swimming is at about 1 cm/sec (Wood and Hargis 1971; Andrews 1979a). These behavioral traits may result in selective tidal transport so that larvae avoid being flushed from the estuary. Generally, larvae are transported toward the head of an estuary against a net downstream flow (Seliger et al. 1982) by using these behavioral responses.

Juveniles

Two to three weeks after spawning, oyster larvae seek a solid surface for attachment (called a set, or the process of setting) and commence crawling in circles (Andrews 1979a). In Long Island Sound, the first set is 18 days after the first spawning (Loosanoff and Nomejko 1951). After attachment with a droplet of liquid cement exuded from a pore in the foot, they lose the velum and foot and are now called spat (newly attached oysters). Shells are preferred as attachment, but stones and other firm surfaces may be used. Spat that set during the first 3 days after metamorphosis may grow faster than those setting later (Losee 1979). Metamorphosis may be delayed if suitable substrate is not located (Newkirk et al. 1977). Burke (1983) defined settlement as the behavior of dropping to the bottom, in contrast to metamorphosis, which is the irreversible developmental process.

Several factors influence the setting behavior of larvae. Hidu and Haskin (1971) suggested that rising temperatures over tidal flats during flood tides stimulate setting. In the laboratory, rising temperature triggered setting (Lutz et al. 1970). Swimming larvae have positive phototaxis, which becomes negative with an increase in temperature (Bahr and Lanier 1981). Light inhibits setting in holding tanks (Shaw et al. 1970) and oysters prefer to set on the undersides of shells (Ritchie and Menzel 1969). More oysters settle in the subtidal zone than elsewhere in Delaware Bay (Hidu 1978).

Oyster larvae usually set in established oyster beds or where shell substrate is present. Crisp (1967) postulated that larvae are attracted to the proteinaceous surface of the periostracum of adult shells and observed that larvae did not settle on

shells that had been treated with bleach. Hidu (1969) demonstrated, however, that a waterborne factor, perhaps a pheromone, stimulates larvae to settle on oyster shells. Currents also influence setting patterns: settlement in Delaware Bay is heaviest where tidal currents cut through salt marshes (Keck et al. 1973). Although high salinities stimulate settlement, mortality increases because oyster predators are more numerous at high salinities (Ulanowicz et al. 1980). However,the number of adult spawners is not correlated with the density of spat produced (MacKenzie 1983). Reduction in the quantity of fresh shells and widespread siltation limits the habitat suitable for setting in most oyster beds in the mid-Atlantic region (MacKenzie 1983).

The time of settlement varies among locations and is generally shorter than that of spawning. In the Niantic River estuary, Connecticut, most larvae settled in July and a few in August (Marshall 1959). In Long Island Sound, settlement is from mid-July to early August and again from late August through September (Loosanoff 1966). Large numbers of larvae sometimes die in mid-summer, perhaps because of blooms of dinoflagellates. In Delaware Bay, larvae settle from around July 4 to early September (Maurer et al. 1971). Peaks in setting in the five tributaries studied occurred mostly in July. In Chesapeake Bay, Maryland, setting is from May to October with a two-week peak, usually in July (Beaven 1955). Different tributaries in Chesapeake Bay have peaks at different times: July in the St. Mary's River, Island Bar and Holland Straits; July, August and September in bars in the open bay; August and September at Wreck Shoal; and July and September at Yorktown Fish Pier and Page's Rock (Andrews 1951). In the James River estuary, Virginia, settlement was from mid-June to mid-October with peaks in mid-August and mid-September (Loosanoff 1932).

Adults

Because adult oysters are sessile, their distribution depends on where the larvae set and on subsequent survival of the spat. Oysters typically live in clumps called reefs or beds, in which they are the dominant organisms. The mass of shells sometimes alters the currents, and increases deposition of particulates so that the local environment is modified.

Adults are often dioecious, but also often change gender as protandrous hermaphrodites (Bahr and Lanier 1981). The gender and the process of sex inversion are genetically determined by perhaps three loci (Haley 1977). Typically the young adults are predominately males; subsequent sex inversion with age increases the number of females. Sex ratios in the James River Estuary, Virginia, change from 90% males at 1 year of age to 80% females in older oysters (Andrews 1979a).

GROWTH CHARACTERISTICS

Oysters grow fastest during their first 3 months of life (Bahr 1976). In their second year, juveniles in Delaware Bay that were 11 to 14 mm long on April 3 were 18 to 22 mm on May 7, 23 to 27 mm on June 5, and 26 to 32 mm on July 2 (Carriker et al. 1982). Whole body weight increased from 0.23 g to 4.0 g in those months. In a review of growth rates in the American oyster, Ingle and Dawson (1952) cited the following sizes at corresponding age: 35 to 75 mm in 6 mo and 100 to 125 mm at 4 years in Long Island Sound; 95 to 106 mm at 1 year in New Jersey; 21 mm at 44 days, 40 mm at 12 mo, and 90 mm at 23 mo in Chesapeake Bay. Oysters in the deep cool waters of Chesapeake Bay grow slower than those in shallow warmer waters (Merrill and Boss 1966). In the Virginia part of Chesapeake Bay oysters weigh 24 g at the end of the

first year, 90 g at year 2, 105 g at 3 years, and 190 g at year 4 (Andrews and McHugh 1957). Instantaneous monthly growth coefficients range from 0.42 to 0.84 (Gillmor 1982). In the mid-Atlantic region, the minimum marketable size of 90 mm is attained in 2 to 5 years.

The growth rate of the oyster is largely governed by temperature, salinity, intertidal exposure, turbidity, and food. Growth ceases during winter, except in Florida, where growth is continuous throughout the year (Butler 1952). Growth of Virginia oysters is slow and the condition factor is low during spawning because energy is used for gamete production instead of production of body biomass (Haven 1962). Oysters expend 48% of their annual energy budget in reproduction (Dame 1976). After spawning, Florida oysters gain weight before they increase in length (Butler 1952). Growth of oysters in Long Island is greatest in August and September after spawning, when glycogen reserves are restored (Loosanoff and Nomejko 1949; Price et al. 1975).

Environmental conditions affect growth. Oysters in a salt pond on Long Island in fluctuating salinity grow faster than those under relatively uniform salinity (Pierce and Conover 1954). Oysters in Maine exposed for a relatively short time during the tidal cycle grow at about the same rate as those continuously submerged (Gillmor 1982). Long exposure to the atmosphere, however, reduces growth; those exposed 20% of the time grow twice as fast as those exposed 60% of the time. Growth rate is directly related to phytoplankton density, and some of the observed differences in rates of growth likely are caused by changes in phytoplankton composition and abundance. In South Carolina, oysters grow faster in nutrient-rich salt ponds than in tidal creeks where primary productivity is lower (Manzi et al. 1977). A Walford plot predicts that oysters in South Carolina would cease growing when 140 mm long (Dame 1971); however, oysters 200 mm long occur.

COMMERCIAL SHELLFISHERIES

The American oyster has traditionally supported a valuable industry along the eastern seaboard (MacKenzie 1983). Today, the commercial areas in the Mid-Atlantic region (Figure 2) are in Long Island Sound, bays along the New Jersey coast, Delaware Bay, bays along the coast of Maryland and Virginia, Chesapeake Bay, and Albemarle Sound of North Carolina. Landings have decreased from about 100 million lb during the 1920's (Matthiessen 1969) to about 25 million lb since the 1960's (Table 1). Oyster landings have remained relatively stable in Chesapeake Bay from 1950-1982, whereas landings in the rest of the mid-Atlantic region have fluctuated more than 10 fold (Table 1); oyster production declined steeply in Chesapeake Bay in 1983-84. Maryland and Virginia are the leading producers of oysters followed by New York (Table 2). Annual landings in New York and New Jersey have fluctuated as much as 50%, but in Connecticut the annual landings have fluctuated from 136,000 lb to 1 million lb, and in Delaware from 8,000 to 501,000 lb. In Long Island Sound, persistent set failure is responsible for the decline in landings since 1920 (Matthiessen 1969). A reduction in the spreading of shells due to an increase in the sale of oysters in the shell is partially responsible for the decline in abundance of oysters in Long Island Sound (MacKenzie 1983).

Oysters are taken by handpicking of clumps from reefs (Bahr and Lanier 1981), hand and patent tonging from boats, and dragging and dredging from boats (Korringa 1976). Dredging has made capture more efficient but it also increases the potential for overharvest and depletion of oyster

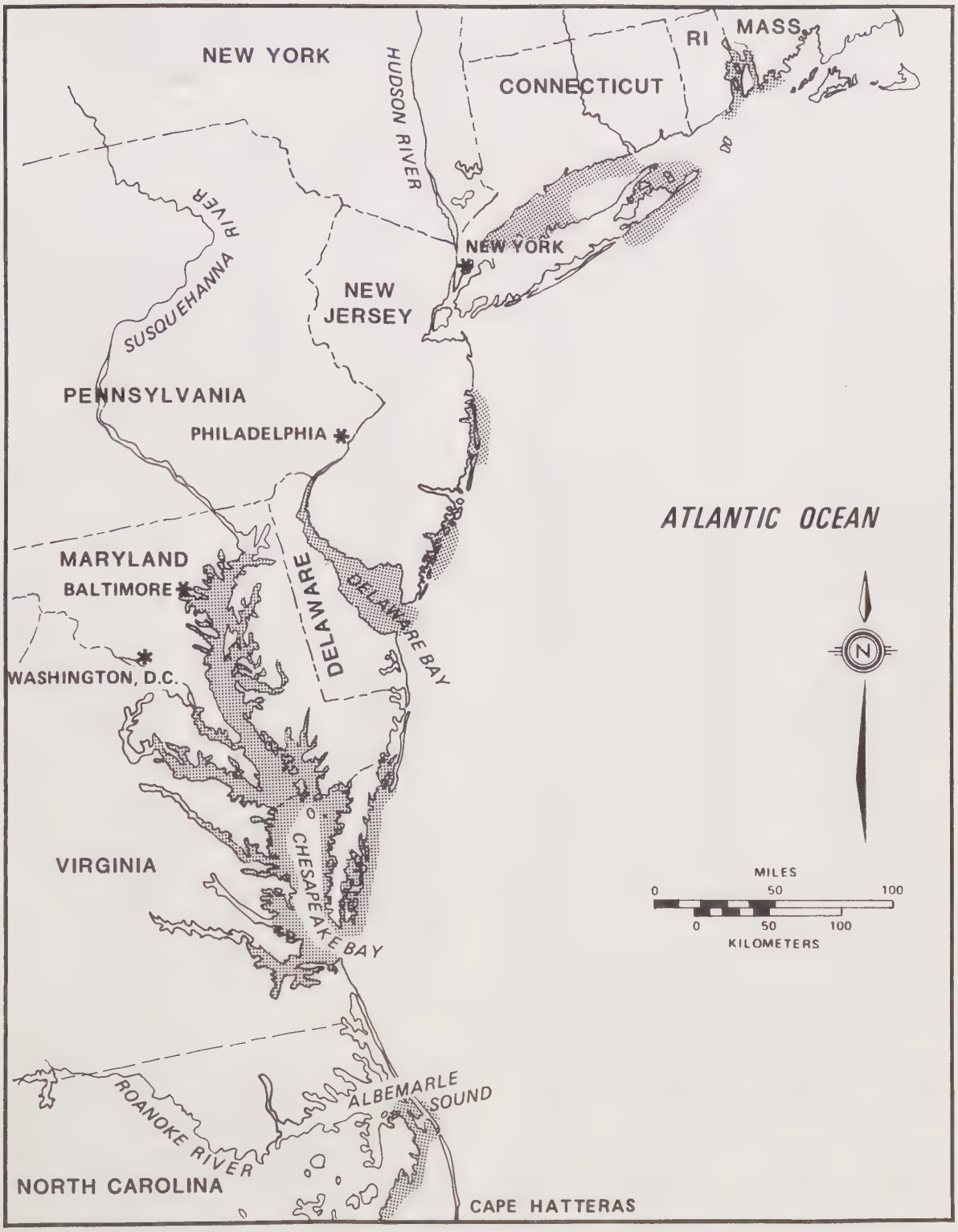

Figure 2. Commercial production areas for the American oyster in the mid-Atlantic.

Table 1. Oyster landings (thousands of pounds meat weight) by geographical region for the years 1950-1982. U.S. Dep. Commerce, NOAA, Natl. Mar. Fish. Serv., Natl. Fish. Statistics Program. Annual summaries of oyster landings, 1950-1982.

Year	New England	Mid-Atlantic	Chesapeake	South Atlantic	Gulf of Mexico
1950	4,727	18,170	29,954	3,033	12,292
1951	1,970	17,410	29,598	3,783	11,519
1952	2,209	16,767	34,418	4,111	14,637
1953	1,038	14,462	36,946	4,019	12,836
1954	735	13,377	41,587	3,811	11,443
1955	619	9,848	39,227	2,260	13,881
1956	506	8,466	37,064	3,656	13,513
1957	405	7,981	34,234	3,069	14,307
1958	276	4,296	37,530	2,651	10,408
1959	387	1,392	33,322	3,516	13,721
1960	500	1,154	27,111	4,119	16,098
1961	453	1,921	27,500	3,984	18,240
1962	294	2,362	19,939	3,850	18,838
1963	452	951	18,274	4,837	24,139
1964	195	1,356	22,098	3,527	23,385
1965	340	757	21,188	4,082	19,156
1966	408	917	21,232	3,657	17,182
1967	323	1,190	25,798	3,160	21,747
1968	195	1,538	22,679	2,965	26,739
1969	152	1,322	22,157	1,830	19,765
1970	190	1,413	24,668	1,626	17,714
1971	190	1,965	25,557	1,846	20,266
1972	129	3,335	24,066	1,868	18,260
1973	181	3,181	25,400	1,656	14,914
1974	644	2,739	25,021	1,841	14,878
1975	600	3,274	22,640	1,585	19,295
1976	201	3,566	20,964	1,704	21,569
1977	905	2,412	18,014	1,861	19,670
1978	887	2,415	21,531	2,138	18,212
1979	1,129	3,038	20,428	2,441	15,289
1980	200	2,635	21,777	2,279	16,548
1981	26	2,396	22,153	2,786	17,079
1982	1,195	2,352	18,134	2,650	24,158

beds. Harvesting by divers has become important in Maryland waters.

The American oyster is the dominant shellfish in mariculture in the United States. In 1980, the yield of cultured oysters was 23 million lb valued at $37 million. This production is equal to 55% of the 1980 U.S. oyster landings. Seed oysters are also harvested for transplanting to water with insufficient natural setting. About 99% of the U.S. seed production comes from Virginia waters (Alford 1975).

The equivalences between different values reported for harvest are: 1

Table 2. Landings (thousands of pounds) of American oyster meats in the mid-Atlantic States 1977-1982. U.S. Department of Commerce, NOAA, Natl. Mar. Fish. Serv., Natl. Fish. Statistics Program. Annual summaries of oyster landings.

	State						Mid-Atlantic	
Year	CT	NY	NJ	DE	MD	VA	total	U.S. total
1977	136	1,059	1,225	128	13,028	4,986	20,562	46,017
1978	852	798	1,553	64	13,470	8,061	24,798	50,968
1979	1,058	1,355	1,675	8	12,290	8,138	24,524	48,071
1980	175	1,378	756	501	14,944	5,833	23,587	49,070
1981	---	1,635	446	315	16,546	5,607	24,549	50,040
1982	1,000	1,474	632	246	11,545	6,589	21,486	54,317

bu = 34 l = 32 kg total weight = 7.8 pints = 3.4 kg meat weight (Pruder 1975).

The market quality of oysters depends on the meat size and taste, which vary with the season. In Florida, the yield of oyster meats per shell is best in March just before spawning and lowest in the summer months during spawning (Rockwood and Mazek 1977). In the lower Chesapeake Bay, meat yields are best in June and again in October and November (Dexter S. Haven, Virginia Inst. of Mar. Sci., pers. comm.). The reduced yields in summer correspond to a reduced condition index following spawning (Hopkins et al. 1954; Lawrence and Scott 1982). Glycogen, which gives oysters their sweet taste, is highest in flesh of Maryland oysters in April and May just before spawning (Sidwell et al. 1979).

Population Dynamics

The vast majority of the eggs and larvae produced by American oysters perish before setting. Following spawning, oyster larvae are abundant plankters; densities have ranged from 2,000 to 5,500/kl in Virginia coastal waters (Andrews 1979a; Seliger et al. 1982), 100 to 17,000/kl in Long Island Sound (Loosanoff and Nomejko 1951), and 24,000/kl in Gardiners Bay of Long Island Sound (Carriker 1959) and in the deeper waters of Delaware Bay (Hidu and Haskin 1971). The concentration of larvae near shore in Delaware Bay was only 1,000/kl. Abundance was greater after high tide in the James River Estuary in Virginia (Andrews 1979a). In the St. Mary's River Estuary in Maryland the numbers per kiloliter were 2,000 to 5,000 straight-hinge larvae, 100 to 1,000 early umbo larvae, and 50 to 200 late umbo larvae (Manning and Whaley 1955).

The daily mortality of larvae in Canada was about 10% (Drinnan and Stallworthy 1979), and for spat in Massachusetts was about 90% monthly (Krantz and Chamberlin 1978).

The density of newly set spat fluctuates greatly from year to year and is different even in adjacent areas. Reported densities range from 0.35-500 spat/shell (Andrews 1949, 1955; Loosanoff and Nomejko 1951; Carriker 1959; Webster and Shaw 1968; Kennedy 1980). Typically there have been 60 spat/bu of natural shells (range 0.6 to 72/bu) in the Maryland portion of Chesapeake Bay (Krantz and Meritt 1977).

Survival of spat in Long Island Sound ranged from 0 to 14% in their

first summer of life (Loosanoff and Engle 1940). Spat mortality of 50% to 70% in Delaware Bay was reduced to 30% to 40% when spat were protected by screens from larger predators (Tweed 1973). Survival of spat to seed (3 to 4 months) in Eastern Bay, Maryland, was less than 10% (Engle 1956). Survival in estuaries of the Choptank River, Maryland, ranges from 1 to 27% through the first season (Webster and Shaw 1968). Of 314 spat per shell that settled, only 14 were still alive at the end of the season in the James River estuary, Virginia (Andrews 1949). Spat survival was less in dense sets than in sparse sets in the James River, Virginia (Andrews 1955) and in Chesapeake Bay (Webster and Shaw 1968). The number of seed per square meter in Long Island Sound was 200 to 10,000; for 1- to 2-year-olds it was 300; and for 3- to 4-year-olds it was 75 (MacKenzie 1981).

The population density of oysters in Delaware Bay was about 70 bu/acre in natural beds and from 10 to 375 bu/acre in planted beds (Maurer et al. 1971). The density of 70 bu/acre was about 80 kg/ha, including shell, or about 800 oysters/ha, assuming an average weight of 100 g. In Chesapeake Bay, the density was about 70 bu/acre in natural beds and 500 bu/acre in planted beds (D. S. Haven, pers. comm.).

American oysters that survive their first year of life are subject to relatively little mortality except that inflicted by shellfishermen or caused by disease outbreaks. In Long Island Sound the annual natural mortality of adults was only 4%, e.g., 77% survived after 4 years (MacKenzie 1981). Adult survival in South Carolina was 85% in a salt pond and 40% in an estuary (Manzi and Burrell 1977). Mortality was size dependent. Mortality of adults 25 to 50 mm long was 19% per month in summer (28% in July), but those 50 to 75 mm long were lost at the rate of 5% per month (near 0% in July) and those greater than 75mm long died at a rate of less than 1% per month (Dame 1976). Survival was 100% in areas protected from heavy waves in North Carolina, and 50% per month if exposed to relatively heavy waves (Ortega 1981). Mortalities were much higher in the areas of Delaware Bay and lower Chesapeake Bay where oysters were infected with MSX disease (Andrews 1968).

ECOLOGICAL ROLE

Oyster larvae feed largely on plankton, particularly small, naked flagellates (Chrysophyta), according to Guillard (1957). At moderate temperatures larval growth is best with a diet of naked flagellates, whereas at temperatures above 27 °C naked algae are scarce and chlorophytes are much more abundant as food (Davis and Calabrese 1964). The larvae, unlike adults, do not consume bacteria (Davis 1953). Oyster larvae are food for a wide variety of filter feeders (Andrews 1979a).

Adult oysters filter large quantities of brackish water and remove naked flagellates. They most effectively filter particles in the 3- to 4-µm size range (Haven and Morales-Alamo 1970). For each gram of dry weight of tissue, an oyster held at 21 °C filters 1.5 l/hr (Palmer 1980). At somewhat higher temperatures about 8 l/hr are filtered (Langefoss and Maurer 1975). The volume of water filtered per hour was 1,500 times the volume of the oyster's body (Loosanoff and Nomejko 1946). The filtration rate is independent of the available food supply, the stage of tide, or time of day. If food is absent, however, the valves are closed most of the time (Higgins 1980). In Chesapeake Bay, oysters ingested the predominate diatom plankton which changes seasonally (Morse 1945). Dinoflagellates, ostracods, small eggs, and terrestrial pollen were also ingested.

The oyster is the dominant species of a diverse community in brackish waters. Over 40 macrofaunal species or groups live in oyster beds (Bahr and Lanier 1981) and the number of species in an oyster community sometimes exceeds 300 (Wells 1961). Oysters were responsible for 88% of the respiration of an oyster reef (Bahr and Lanier 1981).

Oysters have a variety of diseases and parasites and are preyed upon by several carnivores (Galtsoff 1964). The bacteria Vibrio and Pseudomonas sometimes kill oysters. In the laboratory Vibrio exotoxin at 47µg/l kills oyster embryos (Brown and Roland 1984). The protozoan pathogen Perkinsus marinum infects oysters from Delaware to Mexico. The haplosporidian protozoan Minchinia nelsoni is responsible for the disease MSX and Minchinia costalis for SSO (seaside organism) (Andrews 1979b; 1982a). Minchinia nelsoni, common from North Carolina to Massachusetts (Krantz et al. 1972), caused extensive oyster mortality in the Delaware Bay in 1957 and in Chesapeake Bay in 1960 (Andrews 1968). It also killed large numbers of oysters in the bays along the coast of Maryland and Virginia in 1960 (Rosenfield 1971).

Predators often limit the abundance of oysters, especially if salinities are above 15 ppt (MacKenzie 1983). In the mid-Atlantic region, the gastropod oyster drills (Urosalpinx cinerea and Eupleura caudata), the southern oyster drill (Thais haemastoma), the whelk (Busycon canaliculatum), the starfish (Asterias forbesi), and the crab (Cancer irroratus, Callinectes sapidus, and Carcinus maenas) destroy large numbers of oysters (Galtsoff 1964). All sizes of oysters are killed but small sizes are affected most by oyster drills, which bore through the shells with a combination of chemical dissolution of the shell and radular rasping. Small oysters are preyed on by crabs and starfish. The widespread boring sponge Cliona weakens the shell and thus lowers quality (Schlesselman 1955). Spat are preyed upon by the flatworm Stylochus ellipticus (MacKenzie 1970; Christensen 1973). The bay anemone (Diadumene leucolena) consumed 0.6 to 4.9 oyster larvae per minute in the laboratory and also feeds on larvae in the natural environment (Steinberg and Kennedy 1979). Over 100 bay anemones/m^2 have been known to occupy oyster beds in Chesapeake Bay (MacKenzie 1977). The southern oyster drill consumes 2.4 spat/day under optimum conditions (Garton and Stickle 1980). In a study of oyster mortality in Long Island Sound, MacKenzie (1981) estimated that starfish inflicted 25% mortality on spat in 5.5 months, mud crabs 12%, and oyster drills 5%. For adult oysters near Norwalk, New York, starfish cause 3.2% of the annual mortality, oyster drills 0.2%, and suffocation 0.2%. In New Haven, Connecticut, starfish had no impact, oyster drills killed 0.5%/year, and suffocation killed 2.9%/year. The oyster drills are the primary predators of oysters in Chesapeake Bay (Lippson 1973). In the Gulf of Mexico, oysters are preyed on by a variety of other predators (Cake 1983).

Major competitors of the oyster for space on substrate include the slipper shells (Crepidula spp.) and the jingle shells (Anomia spp.) as well as barnacles (Balanus eburneus and Chthamalus fragilis) and other oysters that set on adult shells (MacKenzie 1970; 1983). Shells with heavy fouling by barnacles have only about 25% as many spat as clean shells (Manning 1953). Heavy sets of barnacles reduce the hard surface available for oyster spat and thus reduce oyster settlement (Ingle 1951); therefore oyster spat are limited to areas relatively free of barnacles and bryozoans (Beaven 1955). The mussel Brachiodontes exustus may also compete with oysters (Ortega 1981). Young oysters may be smothered by excreta of polychaete worms of the genus

Polydora, or by excreta of adult oysters (Stenzel 1971). Blooms of red tide (Cochlodinium heterolobatum) at concentrations of 500 cells/ml killed oyster larvae (Ho and Zubkoff 1979). Competition by the slipper shells and barnacles may limit numbers of oysters in Long Island Sound (MacKenzie 1981; 1983). Tunicates and encrusting sponges are also major competitors for space (D. S. Haven, pers. comm.).

ENVIRONMENTAL REQUIREMENTS

The American oyster typically lives in shallow, well-mixed estuaries, lagoons, and nearshore bays, and tolerates widely fluctuating water temperatures, salinities, and suspended solid concentrations (Andrews 1979a). Because of the tolerance of extreme fluctuations in environmental conditions, the environmental requirements of oysters are difficult to define.

Temperature

Differences in thermal requirements of oysters from different areas have led to the postulation that races may be separated on the basis of different temperature requirements (Ahmed 1975). Approximate spawning temperatures for three distinct races were 16 °C for the northern race (New England), 20 °C for the mid-Atlantic race, and 25 °C for the Gulf of Mexico race (Stauber 1950). Menzel (1955) found that ciliary activity continued at 0 °C in the New England oysters but ceased at 6 °C in oysters from the mid-Atlantic. Andrews (1979a) suggested there are other races as well, but genetic studies did not closely support the existence of physiological races (Buroker et al. 1979). All oysters studied by Buroker et al. (1979) were genetically identical, except those from Nova Scotia and Florida. These populations were 82% similar, about the level of similarity between the American and the mangrove oyster, which can successfully hybridize (Menzel 1968). According to Groue and Lester (1982) American oysters in Laguna Madre, Texas, are genetically distinct from four other gulf populations. Measurement of isozymes in genetic studies, however, may not validate these races.

In the mid-Atlantic coastal waters, oysters spawn when water temperatures are somewhat above 20 °C. Gonads do not develop at water temperatures below 10 °C, and 16 °C is needed for gonadal maturation (Loosanoff and Davis 1952). Exposure to a 35 °C water temperature accelerated gametogenesis and spawning, but subsequent spawning in the same season was prevented (Quick 1971). In laboratory tests, embryos developed normally at water temperatures between 20° and 30 °C but abnormalities increased progressively when water temperatures declined to 15 °C or rose to 35 °C (MacInnes and Calabrese 1979). The percentage of abnormal embryos increased from 2% at 25 °C to 12% at 30 °C (Dupuy 1975). The growth of larvae was impaired by water temperatures of 30 °C or more and even a brief exposure for 10 min at 40 °C retarded growth (Hidu et al. 1974). In contrast, a temperature range of 27 to 32 °C is optimum for fastest growth and highest survival of larvae in Long Island Sound (Davis and Calabrese 1964).

Adults tolerate water temperatures from a low of -2 °C in New England to a high of 36 °C in the Gulf of Mexico. At low tide, oysters may be exposed to and survive air temperatures ranging from well below freezing to above 49 °C (Galtsoff 1964). High temperatures sometimes increase the mortality rate; temperatures above 35 °C for an entire tidal cycle may kill some or all oysters (Tinsman and Maurer 1974). The critical thermal maximum for the American oyster is 48 °C (Henderson 1929).

Oysters can tolerate freezing of their tissues, and sometimes revive after thawing (Loosanoff 1965a).

Optimum water temperatures for carrying out various life functions in the adult American oyster are 20 to 30 °C. Optimum temperatures for maximum pumping rates were 20 to 25 °C (Collier 1951) or at 28 to 32 °C (Loosanoff 1958). Growth stops in waters with temperatures below about 8 °C (Price et al. 1975). Oysters at 2 to 7 °C are inactive. The threshold for feeding is 3 °C (Haven and Morales-Alamo 1966). Exposure to unseasonably high temperatures in winter stimulates growth if food is available (Ruddy et al. 1975). Growth is possible between 6 and 32 °C but the optimum is about 26 °C (Galtsoff 1964).

Salinity

Oysters prefer waters of relatively high salinity. When salinity is above about 20 ppt, marine predators flourish and destroy large numbers of oysters. Oysters usually live in brackish waters or in areas of unstable salinity that are unsuitable for marine predators. In upper Chesapeake Bay, for example, spat density was positively correlated with high salinity, whereas oyster harvest was negatively correlated with high salinity (Ulanowicz et al. 1980).

Salinities above 7 ppt are required for spawning (Loosanoff 1948). Embryos developed normally at salinities of 16 to 30 ppt (MacInnes and Calabrese 1979). Larvae tolerated salinities of 3 to 31 ppt (Carriker 1951), but grow fastest and survived best at salinities above 12 ppt (Davis and Calabrese 1964). In Virginia, salinities of 20 to 35 ppt were required for normal embryo development and the optimum was 28 ppt (Castagna and Chanley 1973). In the laboratory, almost no embryos of Long Island Sound oysters developed below 15 ppt; the percentage progressively increased to a salinity of 22.5 ppt (Davis 1958). As salinity increased further to 35 ppt, abnormalities increased, and all died above 40 ppt. Differences in salinity tolerance of larvae are explained by the acclimation of the adults before spawning. Larvae produced from the spawning of Maryland oysters acclimated to the salinity of Long Island Sound (26 ppt) had the same salinity tolerance as larvae from Long Island Sound oysters. Maryland oyster larvae, however, were much more tolerant of low salinities if the parents were acclimated to 9 ppt water (similar to Chesapeake Bay). The larvae from parents adapted to low salinity developed normally at 10 ppt, and most survived at 7.5 ppt. Development stopped at 22.5 ppt, which would be the optimum salinity if the parents had been held at higher salinities.

Most larvae in a New Jersey estuary were in the halocline at salinities above 5 ppt (Carriker 1951). Larvae of Virginia oysters of parents in high salinity water did not metamorphose below 17.5 ppt (Castagna and Chanley 1973), a finding obviously not applicable to populations living in low saline waters. Optimum salinities for the growth of spat in lower Chesapeake Bay were 15 to 22 ppt (Chanley 1957) and in Long Island Sound, 17.5 to 22.5 ppt (Davis 1958). Oysters in Chesapeake Bay did not grow at salinities below 5 ppt (Abbe 1982).

Adult oysters tolerate a salinity range of 5 to 32 ppt. Outside of this range of salinities they discontinue feeding and reproducing. The optimum salinity range in Long Island Sound is 10 to 28 ppt (Loosanoff 1965a) and in Delaware Bay, 14 to 28 ppt (Maurer and Watling 1973). Loosanoff (1965b) found that many oysters survive 3 ppt for 30 days. Large numbers, however, die during prolonged freshwater inflow from the James River, Virginia (Andrews et al. 1959; Andrews 1973). Similar observations were made in Mobile Bay, Alabama (May

1972), and in the Santee River, South Carolina (Burrell 1977). Salinities during high freshwater inflow were below 2 ppt in the Santee River. Many oysters died in the Beaufort Inlet, North Carolina, after exposure to a salinity near 5 ppt for about a month (Wells 1961). Oysters in Louisiana died after 14 days at 6 ppt (Anderson and Anderson 1975). In Delaware Bay, oysters survived salinities as low as 2 ppt (Maurer et al. 1971). The length of time oysters survive low salinities evidently depends on the abruptness of the changes in salinity.

Low salinities inhibit gonadal maturation in oysters in Chesapeake Bay (Butler 1949) and Long Island Sound (Loosanoff 1953). Reproductive failure may be a direct effect of salinity or might be caused by inadequate feeding at low salinity.

Substrate and Current

The preferred habitats in shallow estuarine waters are mud flats and offshore bars (Hidu 1968), and oyster reefs (Bahr and Lanier 1981). Maximum density of spat is on horizontal surfaces (Clime 1976).

Oysters grow equally well on shells, rocky bottoms, or on thick mud, capable of supporting the oysters' weight. Soft muddy substrates may be improved by adding clam or oyster shells. Oyster shells from muddy substrates are more slender than those from hard substrates (Galtsoff 1964). In Delaware Bay mariculture sites, oysters preferred to set on the bottom rather than on panels suspended in the water column, and preferred subtidal waters (Hidu 1978).

Currents are particularly important to the larvae and adults of the American oyster. Larvae are transported by currents. They position themselves in the ebb and flow of tidal currents to remain in estuaries. Excessive currents, however, may prevent settlement (Cake 1983). Since the volume of water immediately above an oyster bed must be completely flushed about 72 times every 24 hr for maximum feeding, oysters require currents (Galtsoff 1964). Tidal flows of 156 to 260 cm/sec or higher are needed for optimum growth in Mississippi (Veal et al. 1972). Currents over oyster bars in Beaufort Inlet and the Newport River estuary in North Carolina were 11 to 66 cm/sec (Wells 1961). Currents of 150 to 600 cm/sec were measured above oyster bars in Delaware Bay (Hidu and Haskin 1971), and 180 cm/sec in Milford Harbor, Connecticut (Prytherch 1929). Turbulent currents that carry sand and pebbles, however, can damage shells by eroding shell surfaces (Galtsoff 1964). A velocity of 150 cm/sec caused unattached oysters to tumble along the bottom of Long Island Sound (MacKenzie 1981). In Delaware Bay, oyster abundance was greatest in areas of scour where current kept the beds free of sediments (Keck et al. 1973). Oysters died in one week if covered with sediment at a water temperature of 20 °C, and in 2 days if the water temperature was 25 °C (Dunnington 1968). Currents are also necessary for removal of pseudofeces and feces (Lund 1957).

Oxygen

In one study, the hourly oxygen consumption was 39 ml/kg for a whole animal including the shell or 303 ml/kg of wet tissue (Hammen 1969). Oxygen consumption increases with increasing temperature; Q_{10} values (the factor by which a reaction velocity is increased by an increase in temperature of 10 °C) ranged from 1.2 to 2.3 for gill tissue and 2.7 to 4.2 for mantle tissue (Bass 1977).

The rate of oxygen consumption by oysters increases as temperature increases and salinities decrease (Figure 3). Oysters exposed to prolonged periods of low salinities closed their shells and died of anoxia

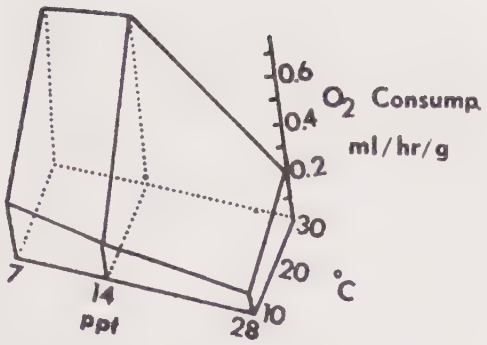

Figure 3. Oxygen consumption in American oyster adults as a function of salinity and temperature (Shumway 1982).

in the James River and Rappahannock River estuaries (Andrews 1982b). Oysters are facultative anaerobes and are able to survive daily exposure to low oxygen. They also are known to survive anaerobically for 3 days after spawning (Galtsoff 1964). Oxygen consumption is zero when the valves are closed (Hammen 1969). In a study in Delaware Bay, oxygen concentrations over oyster reefs ranged from 1 to 12 mg/l (Maurer et al. 1971). The decline in oyster harvest in Chesapeake Bay in recent years may be caused by decreased concentrations of oxygen, although more established factors include the outbreak of MSX disease in 1981-1983, poor spat set for over a decade, and high harvest pressure.

Turbidity and Sedimentation

Oysters tolerate water with large amounts of suspended solids, but the pumping rate decreases with increasing concentrations of suspended solids. Pumping is reduced 70% to 85% over the range 0 to 1 g/l, depending on the nature of the suspended sediment (Loosanoff and Tommers 1948). In the laboratory the growth of larvae was reduced at concentrations of particulates above 0.75 g/l (Davis and Hidu 1969). In natural environments, oysters apparently develop and grow better in waters with more suspended solids in oyster beds than in waters with less suspended particulates (Rhoads 1973). Storms and hurricanes may destroy oyster reefs by covering them with sediment.

Acidity

Oyster embryos develop normally within a pH range of 6.8 to 8.8 and develop abnormally at a pH above 9.0 or below 6.5 (Calabrese and Davis 1966; Calabrese 1972). Larvae tolerate the same pH range as embryos but growth is fastest at a pH of 8.2 to 8.5.

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16. Abstract (Limit: 200 words)

Species profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal aquatic species. They are designed to assist in environmental impact assessment. The American oyster (Crassostrea virginica)is an important commercial and mariculture species. It is the dominant species in many bays and oyster shells form extensive reefs that modify sedimentation and local currents. Spawning occurs repeatedly during warmer months with millions of eggs released. Embryos and larvae are carried by currents throughout the estuaries and oceanic bays where oysters occur. The few surviving larvae cement themselves to solid objects for the remainder of life.

Unable to move, they must tolerate changes in the environment that range from -1.7° to 49 °C, 5 to 30 ppt salainity, and clear to muddy water. The distribution and abundance of adults are limited by marine predators, so that oysters are limited largely to brackish waters.

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